

## The Ecological Role of the Prehensile Tail in White-Faced Capuchins (*Cebus capucinus*)

P.A. GARBER\* AND J.A. REHG

Department of Anthropology, University of Illinois, Urbana, Illinois 61801

**KEY WORDS** prehensile tail; locomotion; posture; feeding ecology; platyrrhines

**ABSTRACT** Prehensile tails appear to have evolved at least twice in platyrrhine evolution. In the atelines, the tail is relatively long and possesses a bare area on the distal part of its ventral surface that is covered with dermatoglyphs and richly innervated with Meissner's corpuscles. In contrast, the prehensile tail of *Cebus* is relatively short, fully haired, and lacks specialized tactile receptors. Little is currently known regarding tail function in capuchins, and whether their prehensile tail serves a greater role in feeding or traveling.

In this paper we examine patterns of positional behavior, substrate preference, and tail use in wild white-faced capuchins (*Cebus capucinus*) inhabiting a wet tropical forest in northeastern Costa Rica. Observational data were collected over the course of 3 months on adult capuchins using an instantaneous focal animal time sampling technique. Differences in the frequency and context of tail use, and the estimated amount of weight support provided by the tail relative to other appendages during feeding/foraging and traveling were used as measures of the ecological role of this specialized organ in capuchin positional behavior. During travel, quadrupedal walking, leaping, and climbing dominated the capuchin positional repertoire. The capuchin tail provided support in only 13.3% of travel and was principally employed during below branch locomotor activities. In contrast, tail-assisted postures accounted for 40.6% of all feeding and foraging records and occurred primarily in two contexts. The tail was used to suspend the individual below a branch while feeding, as well as to provide leverage and weight support in above-branch postures associated with the extraction of prey from difficult to search substrates. A comparison of tail use in *Cebus*, with published data on the atelines indicates that both taxa possess a grasping tail that is capable of supporting the animal's full body weight. In capuchins and howling monkeys, the tail appears to be used more frequently and serves a greater weight-bearing role during feeding than during traveling. In *Ateles*, and possibly *Brachyteles*, and *Lagothrix*, however, the prehensile tail serves a dual role in both feeding and forelimb suspensory locomotion. Additional relationships between white-faced capuchin feeding, positional behavior, extractive foraging techniques, and prehensile tail use are discussed. *Am J Phys Anthropol* 110:325–339, 1999. © 1999 Wiley-Liss, Inc.

The evolution of grasping hands and feet and a divergent hallux bearing a flattened nail occurred early in primate evolution (Cartmill, 1972, 1974). Although the precise

\*Correspondence to: P.A. Garber, Department of Anthropology, University of Illinois, 109 Davenport Hall, 607 S. Mathews Ave., Urbana, IL 61801. E-mail: p-garber@uiuc.edu

Received 13 March 1998; accepted 12 July 1999.

ecological factors that selected for grasping cheiridia remain unclear, several authors have suggested that initial changes in primate prehension were associated with the exploitation of food resources such as ripe fruits, floral nectar, and mobile insect prey located on small, flexible supports (Cartmill, 1972, 1974; Martin, 1990; Sussman, 1991). Over the past 55 million years, numerous primate lineages have evolved additional morphological adaptations of the digits, forelimb, hindlimb, and tail that serve important functions in maintaining balance and weight support in an arboreal setting (Grand, 1972; Rose, 1974; Cant, 1986, 1987, 1992; Fleagle, 1988; Garber, 1991; Hunt, 1991; Gebo, 1996). In many cases, these traits are part of an adaptive complex related to below branch or suspensory capabilities (Napier, 1967; Grand, 1972, 1984; Cartmill and Milton, 1977; Schön-Ybarra and Schön, 1987; Cant, 1992; Gebo, 1996). Despite suggestions that the frequency of suspensory behaviors is expected to increase with body size (Fleagle and Mittermeier, 1980; Rollinson and Martin, 1981), there is evidence that during feeding "most primates extend their foraging radius by hanging below supports with their hands and feet, or combinations of both" (Gebo, 1996:75). In the case of New World monkeys, a small set of genera possess a prehensile or grasping tail. A prehensile tail functions as a fifth limb and enables the animal to suspend its full body weight supported by tail alone, or to use the tail in conjunction with one or more limbs to suspend and maintain balance in an arboreal setting (Rosenberger, 1983; Rosenberger and Strier, 1989; Bergeson, 1996). Although among primates this trait is restricted to certain platyrrhine taxa that range in body weight from 2 to 12 kg, prehensile tails have evolved independently in at least six taxonomically distinct mammalian lineages including marsupials, edentates, rodents, carnivores, pangolins and primates (Alho, 1982; Emmons and Gentry, 1983; Best and Harada, 1985; Lee and Cockburn, 1985; Eisenberg, 1989; and see Bergeson, 1996, for a more complete discussion). Among nonprimates, prehensile tailed mammals range in body size from less than 30 g (the honey

possum, *Tarsipes rostratus*) to over 7,000 g (the anteater, *Tamandua tetradactyla*) (Renfree et al., 1984; Eisenberg, 1989), and differ in positional behavior, foraging methods, diet, fore- and hindlimb anatomy, degree of arboreality, and tail anatomy (Tyndale-Brisco, 1979; Alho, 1982; Renfree et al., 1984; Best and Harada, 1985; MacDonald, 1985; Eisenberg, 1989). The independent evolution of prehensile tails among these diverse mammalian lineages suggests that this adaptation represents an effective solution to a range of problems faced by both larger and smaller animals exploiting an arboreal environment.

Based on genetic and anatomical evidence, prehensile tails appear to have evolved at least twice in platyrrhine evolution (Rosenberger, 1983; Lemelin, 1995; Porter et al., 1997), once in the common ancestor of atelines (*Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*) and again in the lineage leading to the genus *Cebus*. *Cebus* and the atelines represent distinct clades at the family level (Cebidae and Atelidae; Schneider and Rosenberger, 1996). Given differences in tail morphology (see below and Table 1), and molecular and paleontological data indicating that these taxa have not shared a common ancestor for an estimated 20 million years (Schneider and Rosenberger, 1996), the prehensile tail of *Cebus* and the atelines are best interpreted as representing parallel evolutionary adaptations (Rosenberger, 1983; Delson and Rosenberger, 1984; Ford, 1986; Rosenberger and Strier, 1989).

As outlined in Table 1, the ateline tail is absolutely and relatively long, possesses a bare area on the distal part of its ventral surface that is covered with dermatoglyphs and richly innervated with Meissner's corpuscles, and is characterized by a well developed set of muscles associated with caudal flexion and tail extension (Lemelin, 1995). In *Alouatta caraya*, for example, the tail "weighs more than the forelimb and possesses a greater range of motion than either the forelimb or the hindlimb" (Grand, 1977: 222). In contrast, the tail of *Cebus* is relatively short, fully haired, lacks specialized tactile receptors, and differs from atelines in the degree of development of the dorsal and

TABLE 1. Anatomical characteristics of the tails of selected platyrrhine primates<sup>1</sup>

Anatomical traits	<i>Aotus</i>	<i>Saimiri sciureus</i>	<i>Cebus</i>	<i>Alouatta</i>	<i>Ateles</i>
Tail weight as % total body weight	4.2	NA	5.4	5.5–6.5	7.8
Osteology sacral index <sup>2</sup>	NA	77.1	80.7 for increased vascularization and innervation	94.4 for increased vascularization and innervation	121 for increased vascularization and innervation
tail length/head-body length	0.9	1.3 to 1.6	1.0 to 1.2 (apella)	1.1 to 1.25 (seniculus)	1.6 to 1.8 (paniscus)
no. of caudal vertebrae	NA	28	25	27	31
Skin	fully haired tail, no dermatoglyphs or Meissner's corpuscles	fully haired tail, no dermatoglyphs or Meissner's corpuscles	fully haired tail, no dermatoglyphs or Meissner's corpuscles	increased sensitivity: distal ventral third of tail is bare, covered with dermatoglyphs, skin contains Meissner's corpuscles	increased sensitivity: distal ventral third of tail is bare, covered with dermatoglyphs, skin contains Meissner's corpuscles
Muscles					
distal muscle bundles	dorsal and ventral bundles of equal size	dorsal and ventral bundles of equal size	ventral bundles larger than dorsal bundles	ventral bundles larger than dorsal bundles	ventral bundles larger than dorsal bundles
extensor caudae lateralis	cross up to 13 caudal vertebrae	cross up to 13 caudal vertebrae	cross 9 or fewer caudal vertebrae: increased range of tail extension	cross 7 or fewer caudal vertebrae: increased range of tail extension	cross 7 or fewer caudal vertebrae: increased range of tail extension
flexor caudae longus	cross up to 13 or 15 caudal vertebrae	cross up to 13 or 16 caudal vertebrae	cross 7 or 8 caudal vertebrae increased range of tail flexion	cross 7 or 8 caudal vertebrae increased range of tail flexion	cross 7 or 8 caudal vertebrae increased range of tail flexion

<sup>1</sup> Table adapted from Bergeson, 1996. Information from this table taken from Ankel, 1972; Ankel-Simons, 1983; Grand, 1977; MacDonald, 1985; and Lemelin, 1995.

<sup>2</sup> Sacral index is the size of the distal aperture of the sacral neural canal relative to the proximal aperture of the sacral neural canal.

ventral muscle bundles in the tail, and the origin of the transverse processes of the lumbar vertebrae (see Bergeson, 1996) (Table 1). In other aspects of its morphology [i.e. increased size of the ventral relative to the dorsal muscle mass (Grand, 1977), a smaller number of caudal vertebrae crossed by tendons of the flexor muscles (Lemelin, 1995), caudal vertebrae with wide neural arches, and relatively wide transverse processes in the dorsal region of the tail (German, 1982)], the capuchin tail differs from the tail of most other primates and exhibits strong similarities to the ateline tail (Lemelin, 1995). Despite several comparative studies of the anatomy of prehensile tailed platyrrhines (Erikson, 1963; Ankel, 1972; German, 1982; Lemelin, 1995), the degree to which atelines and capuchins use their tails in equivalent

ways remains unclear. In other words, given differences in tail morphology, does the prehensile tail of *Cebus* and atelines fulfill similar ecological roles?

In this paper we examine patterns of locomotor and postural behavior involving tail use in white-faced capuchin monkeys, *Cebus capucinus*. Specifically, we focus on the role of the capuchin tail during both above-branch and below-branch positional activities and address the following questions: 1) What are the general patterns of positional behavior and substrate preference in white-faced capuchins? 2) How frequently is the capuchin prehensile tail used during feeding, foraging, and traveling, and is its use restricted to supports of particular size and orientation? and 3) Under what specific ecological and behavioral conditions

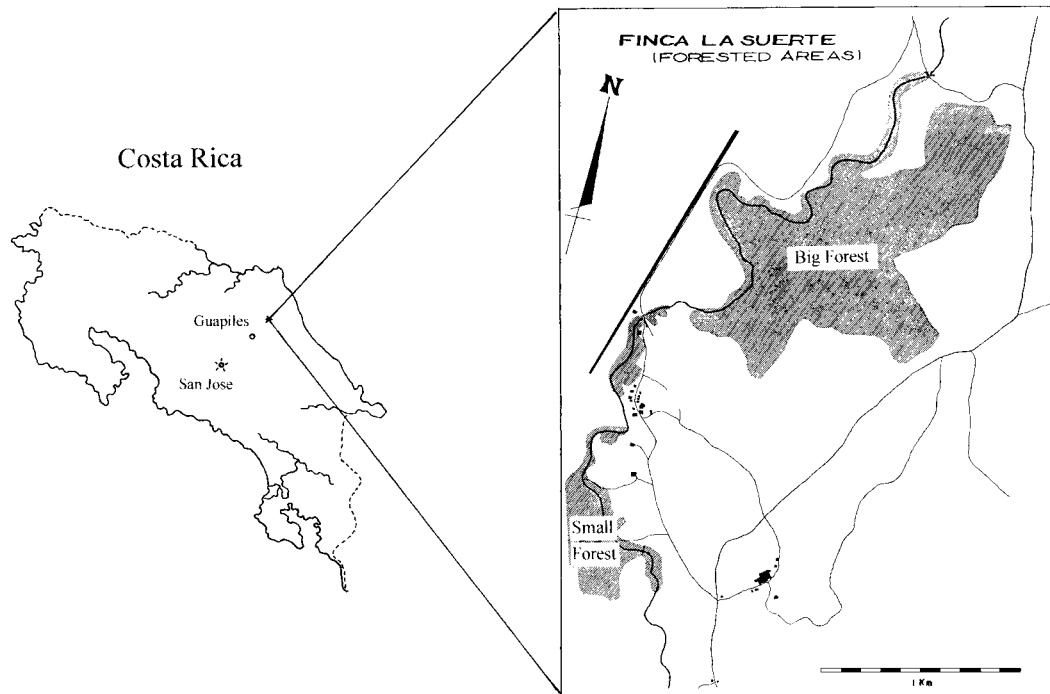


Fig. 1. Map of La Suerte Biological Research Station in northeastern Costa Rica.

does the tail support all or most of the animal's body weight?

## MATERIALS AND METHODS

### The study site

From January through March 1995 data were collected on a habituated group of 10–13 white-faced capuchin monkeys (variation in group size was due to the birth of three infants during the course of the study) at La Suerte Biological Research Station in northeastern Costa Rica (10°26'N, 83°47'W; Fig. 1). The site is characterized by wet tropical lowland forest located along the Río Suerte. Yearly rainfall in this area of Costa Rica averages 3,962 mm, with most precipitation falling during the months of May through December (Sanford et al., 1994). In addition to white-faced capuchins, mantled howling monkeys (*Alouatta palliata*) and black-handed spider monkeys (*Ateles geoffroyi*) inhabit the site.

The home range of the study group was part of a 15–20 ha patch of advanced secondary forest that was selectively logged in the

1970s. Since that time, the forest has been relatively undisturbed and is now part of a protected teaching and research facility. The area utilized by the capuchins is characterized by a closed canopy forest of medium to tall tree stature, high tree and liana density, and few large openings between the crowns of adjacent trees (Garber and Rehg, unpublished data). Approximately 84% of the tree canopy area is characterized by interdigitating branches or lianas that offer continuous pathways for travel. Additional information on the ecology of the area and the capuchin study group is presented in Garber and Paciulli (1997).

Capuchins in our study group were not marked and therefore we were unable to reliably or consistently record data on particular individuals. Based on daily observations we estimate that the group was composed of 2 adult males, 5 adult females, 3 preadults (juveniles or subadults), and 3 infants. Data were collected on adult capuchins between the hours of 05:15 and 17:30 on most days of the study. Based on group

follows in the month prior to this field investigation and group follows during the 3 months of this investigation, these capuchins were found to restrict all of their feeding, foraging, and traveling activities to this small forest patch.

### Behavioral data

Behavioral information on activity pattern and positional behavior of adult capuchins was collected at 2 minute intervals throughout the day using an instantaneous focal animal point sampling technique (see Garber, 1991). A total of 1,873 observations of capuchin positional behavior were recorded (62.4 hours of data). Data were collected on activity (feed, forage, travel, rest, social interaction), location and height in the tree crown, support angle, support size, positional behavior, and use of the tail in weight support. Feeding was defined as any behavioral activity associated with handling, biting, or ingesting a potential food item. In the case of white-faced capuchins this included fruits, insects, vertebrates, nectar, and deadwood. Foraging was defined as localized movement within the crown of a tree that was associated with the visual inspection or manual manipulation of a potential food bearing substrate (nest, hive, deadwood, bark, tree cavity, branch, bromeliad whorls, leaves). Travel was defined as relatively straight-line progression within the crown of a tree or between the crowns of adjacent trees which did not appear to be food related. That is, the focal animal was not observed to search or manipulate any food bearing substrate during movement. During each point sample, special attention was paid to the use of the prehensile tail in posture and locomotion.

The degree and type of weight support provided by the tail was visually estimated based on the position of the tail, the tightness and angle of the tail relative to the body (i.e. a suspended capuchin with a vertically oriented tail wrapped around a branch was judged to support more body weight by the tail than a suspended capuchin with an obliquely or horizontally angled tail), the position of the body relative to supporting branches (i.e. above or below the support), and the number and placement of limbs also

providing support. The tail was scored as providing full support if it was judged to be the sole weight-bearing appendage. Moderate support was scored if the tail was judged to support as much or more weight than any single limb; for example when the capuchin was suspended by a combination of two limbs plus tail. Minimum support was scored if the amount of weight supported by the tail was judged to be less than that borne by any limb; for example when the capuchin tail was loosely draped over a branch while all four limbs were loaded in compression and in contact with a rigid substrate. If the tail was not in contact with a branch, it was scored as providing no support. Cases in which the observer could not clearly see the position of the capuchins' tail or identify its role in weight support were scored as unknown.

Branches of difference size, orientation, and weight-bearing capacity present arboreal animals with different challenges in terms of weight support, stability, and progression through the canopy (Prost, 1965; Cartmill, 1974; Fleagle and Mittermeier, 1980; Cant, 1992). In order to examine relationships between positional behavior, limb placement, tail use, and patterns of substrate utilization, the orientation of the branch(es) used by the focal animal, as well as whether the focal animal was ascending or descending the branch, was recorded. Branch orientation was scored as horizontal (0–15°), oblique (16–74°), vertical (75–90°), or terminal (mass of small branches oriented at various angles to the ground). If the tail was wrapped around a support other than that used by the limbs, the orientation and size of that branch(es) was also recorded. Branch size was scored relative to the size of the animal. Branches that could be grasped by a capuchin hand or foot were recorded as small. Branches that the capuchins were able to encircle with their limbs were considered medium in size, and branches that could not be encircled by the limbs were considered large. We estimate that small branches were  $\leq 5$  cm in circumference, medium branches  $> 5$  and  $\leq 30$  cm in circumference, and large branches  $> 30$  cm in circumference. A description of the



TABLE 2. Definitions of selected locomotor and postural categories<sup>1</sup>


---

<b>Postures</b>	
Bipedal crouch plus tail—a posture in which both hindlimbs are in compression, the knees flexed, one or both arms extended, and the tail is positioned above the body and wrapped around a supporting structure (tail in tension).	
Grasping—a prehensile postural activity using any combination of at least three limbs and possibly the prehensile tail. This differs from bipedal crouch and hindlimb grasp in that at least one forelimb is involved in weight-bearing and therefore serves a role in supporting the animal.	
Suspending by hindlimb plus tail—a form of below branch suspension in which the individual is oriented obliquely or vertically downward, supported solely by the prehensile grasp of one or both hindfeet plus the tail.	
Sitting—a stationary posture in which the haunches support the body with limb and tail placement variable.	
Tail hang—a posture in which the tail is the only appendage supporting the body weight.	
Quadrupedal/Tripodal stand—a posture in which four or three limbs are in compression and the animal is stationary above the support (if the tail was also providing support it was recorded as quadrupedal/tripodal stand plus tail).	
<b>Locomotion</b>	
Climbing—"progression along continuous [vertically and/or obliquely angled] supports using various combinations of three or more limbs" (Fleagle and Mittermeier, 1980:249) and possibly the prehensile tail.	
Leaping—a form of hindlimb dominated propulsion involving an in-air phase of movement which may begin from a stationary posture, slow quadrupedal progression, or quadrupedal running.	
Tail drop leap—a form of leaping in which the animal is suspended primarily by the tail, the limbs are widely abducted at takeoff, and the individual drops to a support below.	
Quadrupedal run—rapid pronograde progression in which all four limbs are in compression (the capuchins adopted a diagonal sequence-diagonal couplet gait during quadrupedal running).	
Quadrupedal walk—slow pronograde progression in which all four limbs are in compression (typically the capuchins adopted a diagonal sequence-diagonal couplet gait during quadrupedal walking).	

---

<sup>1</sup> Appendages include forelimbs, hindlimbs, and tail.

positional (postural and locomotor) categories used in this study is presented in Table 2.

It is important to point out that, as in virtually all studies of positional behavior (e.g. Fleagle and Mittermeier, 1980; Garber, 1991; Gebo and Chapman, 1995; Bergeson, 1996), individuals in our study group were not marked and therefore it was not possible to determine how frequently the same individuals were represented in our point samples. During travel, capuchins move quickly and the focal animal was often lost after only 1 or 2 point samples. When the focal animal was lost from view, the next adult sighted became the focal animal. Therefore our data set is likely to include a large and relatively random set of data points from all adult members in the group. Moreover, we had no cases in which a capuchin traveling during one point sample was still traveling on that same support during the next point sample (2 minutes later). During feeding and foraging, however, individual capuchins often remained in the same tree crown over a longer period of time ( $X = 5.3$  min), and therefore some set of consecutive point samples were likely to be repeated samples of the same individual in the same posture utilizing the same supports. In this regard, our data sets violate assumptions of

random sampling of individuals and sample independence required for most statistical procedures (see Dagosto, 1994, for a discussion of problems associated with statistical tests using point sample data). Repeated sampling of the same individual in the same posture utilizing the same supports accounted for only 5.5% ( $N = 35$ ) of feeding/foraging records. These data points were subsequently removed from the data set and are not included in the analyses presented here. In all statistical analyses a Chi Square Goodness of Fit Test was used to compare behavioral patterns and support preferences during travel vs. feeding and foraging. Given our inability to ensure random sampling of the data, we have conservatively set the alpha level at  $P = 0.01$ .

## RESULTS

### Positional behavior and substrate preference during travel

During travel, slow quadrupedal progression (walking and standing, 52.2%), leaping (24.7%), and climbing (9.4%) dominated the capuchin positional repertoire (Table 3). Overall, 44% of substrates used during travel were small and 44.3% were obliquely angled. Although *C. capucinus* often was observed

TABLE 3. Frequency of positional behaviors recorded during traveling, and feeding and foraging in *Cebus capucinus*

	Travel <sup>1</sup> (N = 780)	Feed/ forage <sup>2</sup> (N = 608)
Quadrupedal walk	49.8	13.6
Leap	24.7	1.3
Climb/grasp	9.4	22.5
Quadrupedal run/bound	8.1	<1
Suspending by hindlimb plus tail	3.2	8.9
Quadrupedal Stand	2.4	12.6
Bipedal crouch plus tail	<1	12.5
Sit	<1	24.5
Tail hang	<1	3.7

<sup>1</sup> The capuchin tail provided support in 13.3% of total travel bouts.

<sup>2</sup> The capuchin tail provided support in 40.6% of total feeding/foraging bouts.

to move through an area quickly, 82% of quadrupedal locomotion was characterized by walking rather than running or bounding. During quadrupedal walking, the most common support types used were medium sized (45.4%) and oblique (60.1%) branches in the interior zones of the tree crown (i.e., nearer to the main axis of the tree than to the periphery).

White-faced capuchins crossed discontinuities in the canopy and gaps between tree crowns principally by leaping. Leaps generally covered a distance of <1–3 m (only 3% of leaps covered a distance greater than 3 m) and were of three main types. *Acrobatic leaps* accounted for 60% of all leaps recorded. These occurred in the periphery of the tree crown and involved the use of small or moderate size supports as a takeoff platform and masses of small terminal branches as a landing platform. Although the distance covered in acrobatic leaps varied from <1 to >5 m, all leaps greater than 1 m in distance (N = 100) recorded in this study were acrobatic leaps. Leaps resulting from uninterrupted, rapid, quadrupedal travel were termed *bounding leaps*. Bounding leaps accounted for 25.8% of capuchin leaping behavior. These leaps are typically short (<1 m) and involved the use of moderate and large sized supports as either landing and/or take-off platforms. In the remaining 11.8% of leaps, a capuchin suspended itself principally by its tail alone or in combination with one or two limbs and dropped to the canopy below (*tail drop leaps*; Fig. 2A).

Unlike other types of leaping behavior, tail drops did not require hindlimb generated propulsive forces and were used to negotiate or span vertical gaps of less than 1 m between adjacent tree crowns.

The capuchin tail provided support in only 13.3% of all travel records. Tail use during travel principally involved below-branch locomotion, such as tail drops and tail assisted hanging and climbing. In 43.3% (45/104) of these tail-assisted positional behaviors, the capuchin prehensile tail was judged to support as much or more weight than any single limb. Branches grasped by the capuchin tail during travel were significantly smaller in diameter than branches used to support the limbs ( $\chi^2 = 2698$ ,  $df = 2$ ,  $P < 0.001$ ; Table 4). This reflected the fact that although large substrates provide stable supports for the hands and feet, they are generally too broad in diameter to be grasped by the capuchin tail. Patterns of substrate orientation used for support by the limbs and the tail during travel were also significantly different ( $\chi^2 = 465$ ,  $df = 3$ ,  $P > 0.001$ ; Table 4). This principally reflected the tendency of capuchins to more commonly wrap their tail around a mass of terminal branches, whereas their hands and feet were more frequently placed on more stable horizontal and oblique supports.

We also examined the relationship between substrate orientation and whether the capuchins climbed up or down the support during travel (Table 5). This was done because movement up a support tends to load the hindlimbs in compression whereas movement down a support is associated with the limbs in tension, and is likely to require a greater contribution of weight support by the tail. As indicated in Table 5, during climbing/grasping/suspension, the capuchins were found to descend supports (61.3%) more frequently than they ascended supports (30.2%;  $\chi^2 = 12.5$ ,  $df = 1$ ,  $P < 0.001$ ). This pattern was substrate specific. Capuchins traveled up and down oblique supports in relatively equal frequency, but exhibited a strong preference to ascend rather than descend single vertical supports (Table 5). It was only when climbing, grasping, and suspending from masses of small branches, that the capuchins showed a clear

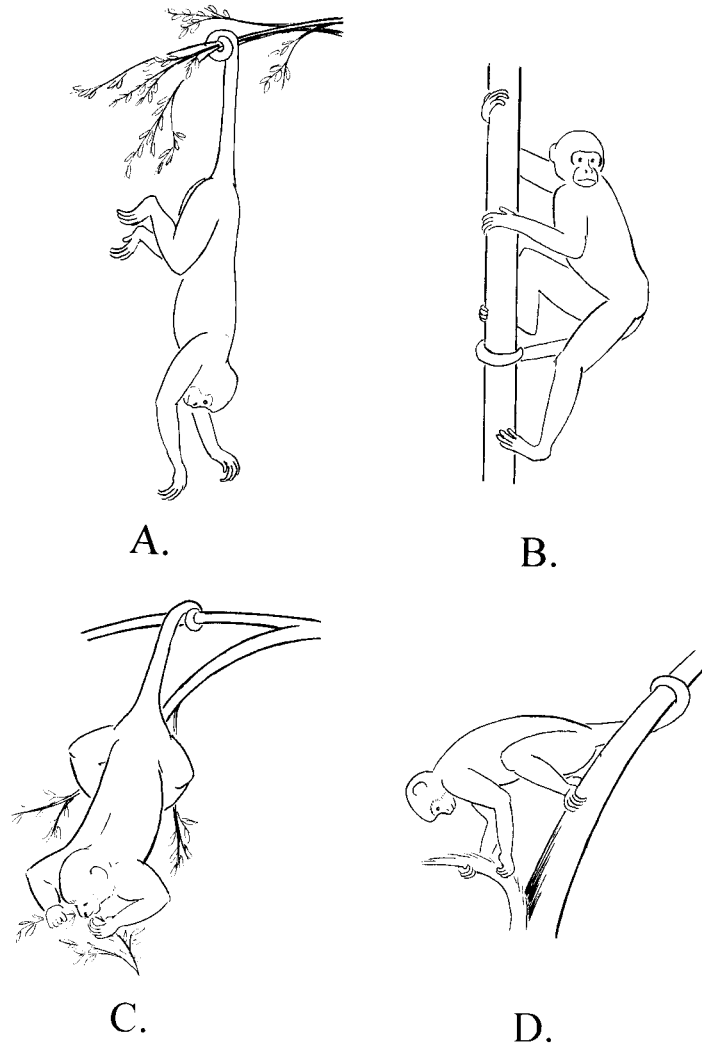


Fig. 2. Tail-assisted positional behaviors adopted by *Cebus capucinus*. **A:** Tail drop leap (animal is depicted just prior to tail release). **B:** Grasping/climbing. **C:** Suspending by hindlimb plus tail. **D:** Tail assisted bipedal crouching.

preference for traveling in a downward direction (Table 5).

#### Positional behavior and substrate preference during feeding and foraging

The diet of white-faced capuchins at La Suerte was composed principally of insects and small vertebrates, soft fruits, and hard-shelled fruits. White-faced capuchins are manipulative foragers and manually explore substrates such as dead leaves, green leaves, bromeliads, dead wood, and tree holes in search of concealed or embedded animal prey. In contrast, fruits are detached from terminal branches and thick stems

(e.g. when feeding on *Dipteryx panamensis* fruits) using one or two hands. Positional behavior during feeding and foraging included sitting (24.5%), quadrupedal walking and standing (26.2%), climbing and grasping (22.5%), tail-anchored bipedal crouching (12.5%) and suspending by hindlimb plus tail (8.9%) (Table 3). Overall, 65.6% of branches used to support the hands and feet during foraging were small and 42.1% were horizontal in orientation (Table 4).

During feeding and foraging, tail-assisted positional behaviors accounted for 40.6% of all activity records. In 46.3% of these cases, the tail was judged to support as much or



TABLE 4. Substrate utilization in *Cebus capucinus*

	Branch size <sup>1</sup>			Branch orientation			
	Small	Medium	Large	Horizontal	Oblique	Vertical	Terminal
Hands and feet <sup>2</sup>							
Feed/Forage (%)							
(N = 602)	65.6	24.9	9.4	42.1	33.5	6.9	17.3
Travel (%) (N = 790)	44.0	38.0	18.0	34.7	44.3	5.6	15.2
Tail							
Feed/Forage (%)							
(N = 169)	68.0	30.1	1.7	36.3	26.1	13.6	23.8
Travel (%) (N = 59)	83.0	16.9	0.0	27.2	19.7	9.0	43.9

<sup>1</sup> See text for explanation of support size and orientation categories.<sup>2</sup> Data are broken down by supports utilized by the hands and feet, and supports utilized by the tail.TABLE 5. Substrate orientation<sup>1</sup> during climbing, grasping, and suspensory positional behaviors in *Cebus capucinus* during traveling and feeding/foraging

	Branch Orientation					%
	Horizontal	Oblique	Vertical	Terminal	Total	
Travel: climb/grasp/suspension						
Up <sup>2</sup>	0	15	18	3	36	30.2
Down	8	18	0	47	73	61.3
Across	2	0	1	7	10	8.4
Total	10	33	19	57	119	
(%)	8.4	27.7	15.9	47.8		
Feed/Forage: climb/grasp/suspension						
Up	0	36	23	9	68	29.7
Down	0	32	10	76	118	51.5
Across	22	4	2	15	43	18.7
Total	22	72	35	100	229	
(%)	9.6	31.4	15.2	43.6		

<sup>1</sup> See text for explanation of orientation categories.<sup>2</sup> The terms up, down, and across refer to the position of the capuchins' body and direction of progression relative to the plane of the ground.

more weight than any single limb. Tail support occurred principally in the context of postural activities such as suspending by hindlimbs plus tail, tail-assisted bipedal crouching, and climbing and grasping in which the hands were removed from a primary role in weight support (Table 3 and Fig. 2C, D). In 26.8% of cases (155/578), the tail prehension allowed the forager to suspend itself below while manually extracting and manipulating food items from difficult-to-search substrates and terminal branches. In 19.3% of cases (112/578) the tail served an important weight bearing role providing full or moderate support (see Methods) in above branch feeding/foraging postures. In these instances, the tautness and position of the tail suggested that strong flexion of the caudal musculature acted as an anchor allowing the capuchin to shift its body weight forward in order to reach, manipulate, and break open with force, tree branches, hard-

shelled fruits, and strip tree bark. Suspension by the tail alone accounted for 3.7% of positional behavior during feeding/foraging.

The frequencies of small, medium, and large sized branches grasped by the capuchin tail during feeding/foraging were significantly different than the frequencies of small, medium, and large sized branches used to support the limbs ( $\chi^2 = 239$ ,  $df = 2$ ,  $P < 0.001$ ). We do note, that as in travel, this difference was driven by the fact that the capuchin tail rarely grasped around large branches. Large branches accounted for 9.4% of the substrates used by the capuchins for fore- and/or hindlimb support, and only 1.7% of tail support (Table 5). The orientation of branches grasped by the tail during feeding/foraging also differed significantly from the orientation of branches used to support the body and limbs ( $\chi^2 = 69$ ,  $df = 3$ ,  $P > 0.001$ ; Table 4). A major difference between tail and limb postures during feeding was the greater

TABLE 6. Relative degree of weight support provided by the Capuchin tail during feeding and foraging

Food type	Total tail support	Full	Mod-erate	Min-imum	None
Fruit (N)	49	26	8	15	41
Animal prey (N)	172	74	43	55	284
Total	221	100	51	70	325
(%)	40.4	18.4	9.3	12.8	59.5

tendency for the tail to grasp vertical branches and terminal branches for support (Table 4).

When adopting climbing/grasping/suspensory positional behaviors during feeding, the capuchins tended to orient their body in a downward direction (Table 5;  $\chi^2 = 13.4$ ,  $df = 1$ ,  $P < 0.001$ ). As during travel, they tended to be positioned up vertical supports, down terminal supports, and to ascend and descend oblique supports in relatively equal frequency. During those feeding behaviors in which the tail was judged to support as much weight as any single limb, the capuchins were most commonly oriented downward on terminal branches or perpendicular to the long axis of a horizontal branch (Table 5; analogous to what is described as bridging behavior; see Gebo, 1992; Bergeson, 1996).

#### Prehensile tail use and diet

Given that tail use was more common during feeding/foraging than during traveling, we examined relationships between positional behavior and the exploitation of different food types. White-faced capuchins often were observed to forage for embedded prey. Foraging substrates were scanned visually for indications of prey activity, and then either manually examined or abandoned in search of other foraging opportunities.

The capuchin prehensile tail provided support in 54.4% (49/90) of fruit feeding activities, and 37.7% of animal prey feeding activities (Table 6). During fruit feeding, the tail was judged to provide as much or more support as any single limb 28.8% of the time. In contrast, when exploiting insect and vertebrate prey, the tail was judged to provide as much or more support than any single limb in only 16.2% of cases. This occurred principally during episodes of destructive foraging (87.5%) when the focal animal ex-

ploited prey that were embedded in tree holes, and bromeliad whorls, or associated with substrates that required stripping of bark. La Suerte white-faced capuchins devoted 84% of feeding and foraging time to the exploitation of insect and vertebrate prey. As a result, 74% (74/100) of all observations in which the prehensile tail played a substantial role in weight support during feeding and foraging, the capuchin was exploiting animal prey (Table 6).

#### DISCUSSION

Along with *Alouatta*, *Ateles*, *Lagothrix*, and *Brachyteles*, *Cebus* represents the only other known primate taxa to have evolved a prehensile tail. Whereas the atelines are reported to weigh between 5 and 12 kg, the five extant capuchin species are smaller in size and weigh between 2 and 3.5 kg (Ford and Davis, 1992). Despite numerous studies of capuchin ecology and behavior (Janson, 1988, 1990; Chapman and Fedigan, 1990; Fedigan, 1990, 1993; Rose, 1994a,b; Fedigan et al., 1996; Janson and Di Bitetti, 1997), there are few quantitative published accounts of posture, locomotion, and tail use in the genus *Cebus* (but see Fleagle and Mittermeier, 1980; Fleagle et al., 1981; Fontaine, 1990; Gebo, 1992; Bergeson, 1996). In this paper quantitative information is presented on positional behavior and tail use in white-faced capuchin monkeys (*Cebus capucinus*) inhabiting a wet tropical forest in Costa Rica. The data indicate that these monkeys are characterized by a prehensile tail that provides support during above and below-branch locomotor and postural behaviors. Capuchins can support their entire body weight using their tail alone; however, the tail was most commonly used in combination with two or three limbs, often both hindlimbs.

At La Suerte, the capuchins used tail-assisted positional behaviors more frequently during feeding and foraging (40.6%) than during traveling (13.3%). The prehensile tail bore as much or more weight than any limb in approximately 19% of all feeding/foraging records. The capuchins were observed to use their tail as an anchor during above-branch feeding activities in which the hindlimbs were positioned on stable supports and the

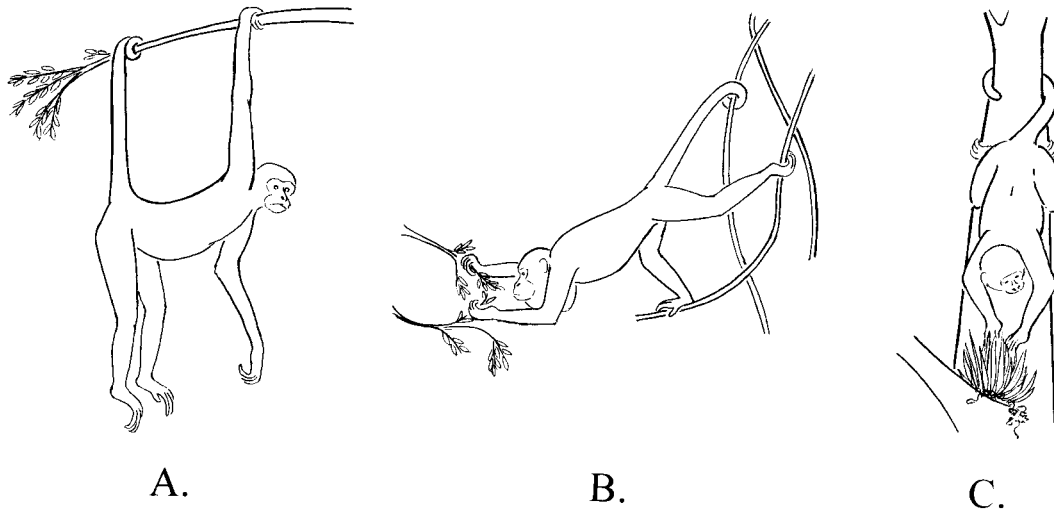


Fig. 3. Common tail-assisted positional behaviors in *Alouatta* (A), *Ateles* (B), and *Cebus* (C). A and B are adapted from photos, diagrams, and descriptions in the literature on Ateline positional behavior from sources such as Mittermeier, 1978; Fleagle, 1988; and Youlatos and Gasc 1994.

forelimbs positioned well in front of the body. In this feeding posture, it appeared that active flexion of the caudal musculature played an important role in supporting much of the animals' body weight. This posture was often associated with faunivory, as individuals manipulated dead wood and epiphytic plants in order to acquire concealed animal prey (Fig. 3C).

During suspension, tail support facilitated below-branch feeding from terminal supports while freeing the hands to collect and extract food items from difficult to reach substrates. Although the tail was used during travel and in other behavioral contexts, based on frequency of use and its role in weight bearing, the capuchin tail was found to serve a primary role in feeding and foraging. These results are generally consistent with other studies of positional behavior in white-faced capuchins (Fontaine, 1990; Gebo, 1992; Bergeson, 1996).

Bergeson (1996:180) reports that white-faced capuchins at two sites in Costa Rica (La Selva and Santa Rosa) frequently adopted what he terms "an inverted bipedal posture" (analogous to our bipedal crouch plus tail) when exploiting palm fruits, which are located on the central axis (trunk) of the tree. When adopting this foraging posture, the capuchin tail is positioned above the

body and wrapped around a vertical trunk, the hindlimbs are in compression, the knees flexed, and the animal's center of gravity is shifted forward (similar to Fig. 3C). In Bergeson's (1996) study, an inverted bipedal posture accounted for 7% of capuchin feeding and foraging behavior. Palms were a major fruit resource used by these capuchins, and he argues that an important function of the capuchin prehensile tail is to facilitate access to these trunk-associated resources. Palms were uncommon in the home range of our study group at La Suerte, and we did not observe capuchins to feed on this resource. We did, however, observe capuchins using this posture repeatedly (12.5% of feeding and foraging activities) to manipulate and extract insect and vertebrate prey during episodes of destructive foraging.

Overall, it appears that the prehensile tail in *C. capucinus* serves a broad adaptive role in both above- and below-branch foraging, providing access to resources located on small and medium sized supports in the perimeter and central regions of the tree crown. Tail plus hindlimbs prehensile postures extend the capuchin's feeding sphere enabling the forager to utilize a more extensive set of small branches from which to feed (Grand, 1972). In addition, the capuchins use their tail as an anchor or counterbalance

during certain above-branch feeding activities on relatively stable supports. These tail-assisted postures are associated with the exploitation of both concealed and embedded vertebrate and invertebrate prey, as well as palm fruits that are located near the main axis of the tree trunk.

### Comparisons in tail-use among *Cebus*, *Ateles*, and *Alouatta*

Field studies on positional behavior and tail use in atelines offer an important starting point for addressing questions concerning the ecological role of the prehensile tail in *Cebus*. A review of the behavioral literature indicates that in *Ateles*, tail-assisted locomotor and postural behaviors such as climbing, bridging, arm swinging, and hanging dominate the spider monkey positional repertoire (Mittermeier, 1978; Cant, 1986; Fontaine, 1990; Bergeson, 1996; Cant et al., 1996). Tail use in all species of *Ateles* has been closely linked to forelimb suspensory locomotion (arm swinging or brachiation) as a specialized mode of travel (Fig. 3A; Mittermeier, 1978; Rosenberger and Strier, 1989; Turnquist et al., 1997). A recent kinematic analysis of spider monkey and woolly monkey locomotion indicates that during forelimb suspensory locomotion, the tail acts to support the entire body weight of the animal (Turnquist et al., 1997). Although considerably less quantitative field data are available on positional behavior in *Lagothrix* and *Brachyteles*, woolly monkeys and woolly spider monkeys also are reported to frequently employ tail-assisted forelimb suspensory locomotion during travel, as well as tail-assisted forelimb suspensory postures during feeding (Nishimura et al., 1988; Ramirez, 1988; Strier, 1992; Cant et al., 1996; Turnquist et al., 1997).

Studies of *Alouatta* indicate a very different pattern of positional behavior. All species of howlers studied (*A. seniculus*, *A. palliata*, *A. pigra*, *A. caraya*) are described as slow arboreal quadrupeds that also engage in frequent climbing and bridging. In *A. seniculus* (Fleagle and Mittermeier, 1980), *A. palliata* (Mendel, 1976; Gebo, 1992; Bergeson, 1996) and *A. caraya* (Bicca-Marques and Calegario-Marques, 1995) slow quadrupedal walking accounted for between 50%

and 80% of the positional behaviors employed during travel. Unlike *Ateles*, forelimb suspension, tail-assisted arm swinging, and other forms of below branch travel are rarely reported in howlers (Schön Ybarra, 1984; Cant, 1986; Gebo, 1992; Bicca-Marques and Calegario-Marques, 1995; Bergeson, 1996).

During feeding (Fig. 3B), howlers engage in frequent bouts of climbing and suspensory behavior on "small supports where the monkeys make extensive use of their prehensile tails" (Fleagle and Mittermeier, 1980: 305). In addition, tail-assisted suspension is used by red howlers (*Alouatta seniculus*), mantled howlers (*A. palliata*), and black and blond howlers (*A. caraya*) during resource exploitation [17% of all feeding counts in red howlers (Schön Ybarra, 1984); 15–20% of feeding in mantled howlers (Mendel, 1976; Gebo, 1992); and 32% of feeding in black and blonde howlers (Bicca-Marques and Calegario-Marques, 1993)]. Youlatos and Gasc (1994:76) also describe a form of tail-assisted vertical descent during foraging on small to large sized supports in *A. seniculus* in which the tail is loaded in tension and "is essential in controlling progression and direction of movement." In all studies of howler positional behavior, the tail is reported to play a more frequent weight-bearing role during feeding than during traveling (Mendel, 1976; Fleagle and Mittermeier, 1980; Schön Ybarra 1984; Gebo, 1992; Youlatos and Gasc, 1994; Bergeson, 1996).

The behavioral evidence for *Cebus*, *Alouatta*, and *Ateles* is consistent with the suggestion that the prehensile tail plays an important role in feeding ecology, posture, and locomotion in all three taxa. Differences in tail and vertebral morphology, and positional behavior among genera, however, suggest that the platyrrhine prehensile tail has come to serve related but different functions in each taxa. Although clearly possessing an ateline-like tail (Table 1), the prehensile tail of *Alouatta* is only moderately elongate and the lumbar region of the vertebral column is less reduced than in *Ateles*, *Brachyteles*, and *Lagothrix* (Erikson, 1963; Johnson and Shapiro, 1998). Differences between *Alouatta* and atelins is reported to reflect a derived condition in *Ateles*, *Brachyteles*, and *Lagothrix* associated with the evolution of tail-

assisted forelimb suspensory locomotion (Rosenberger and Strier, 1989). In contrast *Cebus* possesses a relatively short and fully haired prehensile tail. However, in other aspects of vertebral and tail anatomy, *Cebus* more closely resembles atelines than other cebines [i.e. *Saimiri* and *Aotus* (the present classification of *Aotus* as a cebine remains unclear)]. These include a reduced lumbar region (Johnson and Shapiro, 1998), increased size of the ventral muscle bundles (Grand, 1977), a smaller number of caudal vertebrae crossed by tendons of the flexor muscles (Lemelin, 1995), caudal vertebrae with wide neural arches, and relatively wide transverse processes in the dorsal region of the tail (German, 1982). Data collected in this study suggest that frequent use of tail-assisted hindlimb suspensory behaviors and patterns of climbing down and or across small supports may account for many similarities in ateline and *Cebus* tail morphology (see Johnson and Shapiro, 1998, for a similar interpretation). Specifically, in white-faced capuchins, the tail appears to be used more frequently and serves a greater weight-bearing role during below-branch feeding and foraging than during traveling (Fleagle and Mittermeier, 1980; Schön Ybarra, 1984; Fontaine, 1990; Bergeson, 1996). In addition, the capuchin prehensile tail also appears to serve an important mechanical role in above-branch feeding postures associated with the exploitation of insects, small vertebrates, and hard-shelled fruits.

### CONCLUSIONS

We conclude that the prehensile tail in *Cebus capucinus* serves a primary role in weight support during feeding and foraging (40.6% of activity records). In white-faced capuchins, the prehensile tail provided support in a several above-branch (anchor) and below-branch (suspension) feeding/foraging postures. In contrast, the tail provided weight support in only 13% of travel. In this regard, *Cebus capucinus* resembles species of the genus *Alouatta*, in which the tail is reported to be used more frequently and provide greater weight support during feeding and foraging than during traveling. In *Ateles*, *Brachyteles*, and *Lagothrix*, however, the prehensile tail is reported to play critical

roles in both tail-assisted forelimb suspensory locomotion (travel) and in food procurement.

Little is known regarding patterns of positional behavior and tail prehension in the remaining four capuchin species. These species differ from *C. capucinus* in body size, diet, and modes of habitat exploitation (Ford and Davis, 1992; Janson, 1988, 1990; Daegling, 1992; Ford and Hobbs, 1996). Quantitative behavioral and biomechanical studies are needed to more fully understand relationships between posture, locomotion, feeding ecology, and anatomy within this genus.

### ACKNOWLEDGMENTS

A draft of this paper was presented at the Annual Meetings of the American Association of Physical Anthropologists, April 5, 1997, St. Louis, Missouri. Lisa Paciulli assisted in data collection. Discussions with Dr. Steven Leigh provided helpful insight into appropriate statistical tests used in our analyses. We greatly thank the three anonymous reviewers and journal editor for their helpful comments and suggestions for improving the manuscript. Use of La Suerte Biological Field Station was provided through the generosity of the Molina Family. We especially thank Rene Molina, Lillian Molina, Alvaro Molina, and Federico Molina for their friendship, assistance, and logistical support in the field. As always PAG thanks Sara and Jenni for teaching me about the development of locomotor skills in small bodied primates. Figure 1 was prepared by Ricardo Vásquez.

### LITERATURE CITED

- Alho CJR. 1982. Brazilian rodents: their habitats and habits. In: Mares AM, Genoways HH, editors. Mammalian biology in South America, Vol. 6. Pittsburgh: University of Pittsburgh. pp 143–166.
- Ankel F. 1972. Vertebral morphology of fossil and extant primates. In: Tuttle RH, editor. The functional and evolutionary biology of primates. New York: Aldine, Atherton. pp 223–240.
- Ankel-Simons F. 1983. A survey of living primates and their anatomy. New York: MacMillan.
- Bergeson DJ. 1996. The positional behavior and prehensile tail use of *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*. Ph.D. Dissertation, Washington University, St. Louis.
- Best RC, Harada AY. 1985. Food habits of the silky anteater (*Cyclopes didactylus*) in the Central Amazon. *J Mammal* 66:780–781.
- Bicca-Marques J, Calegari-Marques C. 1993. Feeding



- postures in the black howler monkey, *Alouatta caraya*. *Folia Primatol* 60:169–172.
- Bicca-Marques J, Calegario-Marques C. 1995. Locomotion of black howlers in a habitat with a discontinuous canopy. *Folia Primatol* 64:55–61.
- Cant JGH. 1986. Locomotion and feeding postures of spider and howling monkeys: field study and evolutionary interpretation. *Folia Primatol* 46:1–14.
- Cant JGH. 1987. Effects of sexual dimorphism in body size on feeding postural behavior of Sumatran orangutans (*Pongo pygmaeus*). *Am J Phys Anthropol* 74:143–148.
- Cant JGH. 1992. Positional behavior and body size of arboreal primates: a theoretical framework for field studies and an illustration of its application. *Am J Phys Anthropol* 88:273–284.
- Cant J, Rose M, Schmitt D, Turnquist J, Youlatos D. 1996. Field and controlled observations of the positional behavior of *Lagothrix* and *Ateles*. *Am J Phys Anthropol Suppl* 22:79.
- Cartmill M. 1972. Arboreal adaptations and the origin of the order Primates. In: Tuttle R, editor. *The functional and evolutionary biology of primates*. Chicago: Aldine Atherton. pp 97–122.
- Cartmill M. 1974. Pads and claws in arboreal locomotion. In: Jenkins F, editor. *Primate locomotion*. New York: Academic Press. pp 45–83.
- Cartmill M, Milton K. 1977. The loriform wrist joint and the evolution of “brachiating” adaptations in the Hominoidea. *Am J Phys Anthropol* 47:249–272.
- Chapman CA, Fedigan LM. 1990. Dietary differences between neighboring *Cebus capucinus* groups: local traditions, food availability, or responses to food profitability. *Folia Primatol* 54:177–186.
- Daegling DJ. 1992. Mandibular morphology and diet in the genus *Cebus*. *Int J Primatol* 13:545–570.
- Dagosto M. 1994. Testing positional behavior of Malagasy lemurs: a randomization approach. *Am J Phys Anthropol* 94:189–202.
- Delson E, Rosenberger AL. 1984. Are there any anthropoid primate “living fossils”? In: N Eldredge, Stanley S, editors. *Living fossils*. New York: Fischer. pp 60–61.
- Eisenberg JF. 1989. *Mammals of the Neotropics: The Northern Neotropics*. Chicago: The University of Chicago Press.
- Emmons LH, Gentry AA. 1983. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *American Naturalist* 121:513–524.
- Erikson G. 1963. Brachiation in New World monkeys and in anthropoid apes. *Symp Zool Soc Lond* 10:135–164.
- Fedigan LM. 1990. Vertebrate predation in *Cebus capucinus*: meat-eating in a Neotropical monkey. *Folia Primatol* 54:196–205.
- Fedigan LM. 1993. Sex differences and intersexual relations in adult white-faced capuchins, *Cebus capucinus*. *Int J Primatol* 14:853–877.
- Fedigan LM, Rose LM, Avila RM. 1996. See how they grow: tracking capuchin monkeys (*Cebus capucinus*) populations in a regenerating Costa Rican dry forest. In: Norconk M, Rosenberger AL, Garber PA, editors. *Adaptive radiation of Neotropical primates*. New York: Plenum Press. pp 289–307.
- Fleagle JG. 1988. *Primate adaptation and evolution*. New York: Academic Press.
- Fleagle JG, Mittermeier RA. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *Am J Phys Anthropol* 52:301–314.
- Fleagle JG, Mittermeier RA, Skopec A. 1981. Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Surinam. *Primates* 22:361–367.
- Fontaine R. 1990. Positional behavior in *Saimiri boliviensis* and *Ateles geoffroyi*. *Am J Phys Anthropol* 82:485–508.
- Ford SM. 1986. Systematics of the New World monkeys. In: Swindler DR, Erwin J, editors. *Comparative Primate Biology*. Vol 1. Systematics, Evolution and Anatomy. New York: Alan R. Liss. pp 73–135.
- Ford SM, Davis L. 1992. Systematics and body size: implications for feeding adaptations in New World monkeys. *Am J Phys Anthropol* 88:415–468.
- Ford SM, Hobbs DG. 1996. Species definition and differentiation as seen in the postcranial skeleton of *Cebus*. In: Norcon M, Rosenberger AL, Garber PA, editors. *Adaptive radiations of Neotropical primates*. New York: Plenum Press. pp 229–249.
- Garber PA. 1991. A comparative study of positional behavior in three species of tamarin monkeys. *Primates* 32:219–230.
- Garber PA, Paciulli LM. 1997. Experimental field study of spatial memory and learning in wild capuchin monkeys (*Cebus capucinus*). *Folia Primatol* 68:236–253.
- Gebo DL. 1992. Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *Am J Primatol* 26:277–290.
- Gebo DL. 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *Am J Phys Anthropol* 101:55–92.
- Gebo DL, Chapman CA. 1995. Positional Behavior in five sympatric Old World monkeys. *Am J Phys Anthropol* 97:49–76.
- German R. 1982. The functional morphology of caudal vertebrae in New World monkeys. *Am J Phys Anthropol* 58:453–459.
- Grand TI. 1972. A mechanical interpretation of terminal branch feeding. *J Mammal* 53:198–201.
- Grand TI. 1977. Body weight: its relations to tissue composition, segment distribution, and motor function. I. Interspecific comparisons. *Am J Phys Anthropol* 47:211–240.
- Grand TI. 1984. Motion economy within the canopy: four strategies for mobility. In: Rodman PS, Cant JGH, editors. *Adaptations for foraging in nonhuman primates*. New York: Columbia University Press. pp 54–72.
- Hunt KD. 1991. Positional behavior in the Hominoidea. *Int J Primatol* 12:95–114.
- Janson CH. 1988. Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour* 105:53–76.
- Janson CH. 1990. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys *Cebus apella*. *Anim Behav* 40:922–934.
- Janson CH, Di Bitetti MS. 1997. Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behav Ecol Sociobiol* 41:17–24.
- Johnson SE, Shapiro LJ. 1998. Positional behavior and vertebral morphology in atelines and cebines. *Am J Phys Anthropol* 105:333–354.
- Lee AK, Cockburn A. 1985. *Evolutionary Ecology of Marsupials*. Cambridge: Cambridge University Press.
- Lemelin P. 1995. Comparative and functional myology of the prehensile tail in New World monkeys. *J Morphol* 224:1–18.
- MacDonald D. 1985. *The Encyclopedia of Mammals*. New York: Facts on File.
- Martin RD. 1990. *Primate Origins and Evolution*. Princeton, N.J.: Princeton University Press.
- Mendel F. 1976. Postural and locomotor behavior of *Alouatta palliata* on various substrates. *Folia Primatol* 26:36–53.
- Mittermeier RA. 1978. Locomotion and posture in *Ateles*

- geoffroyi* and *Ateles paniscus*. *Folia Primatol.* 30:161–193.
- Napier JR. 1967. Evolutionary aspects of primate locomotion. *Am J Phys Anthropol* 27:333–342.
- Nishimura A, da Fonseca GAB, Mittermeier RA, Young AL, Strier KB, Valle CMC. 1988. The Muriqui, genus *Brachyteles*. In: Mittermeier RA, Rylands AB, Coimbra-Filho A, da Fonseca GAB, editors. *Ecology and behavior of neotropical primates*, vol. 2. Washington, DC: World Wildlife Fund. pp 577–610.
- Porter CA, Page SL, Czelusniak J, Schneider H, Schneider MPC, Sampaio I, Goodman M. 1997. Phylogeny and evolution of selected primates as determined by sequences of the e-globin locus and 5' flanking region. *Int J Primatol* 18:261–296.
- Prost JH. 1965. A definitional system for the classification of primate locomotion. *Am Anthropol* 67:1198–1214.
- Ramirez M. 1988. The Woolly monkeys, genus *Lagothrix*. In: Mittermeier RA, Rylands AB, Coimbra-Filho A, da Fonseca GAB, editors. *Ecology and behavior of neotropical primates*, vol. 2. Washington, DC: World Wildlife Fund. pp 539–576.
- Renfree MB, Russel EM, Wooller RD. 1984. Reproduction and life history of the honey possum, *Tarsipes rostratus*. In: Smith AP, Hume ID, editors. *Possum and gliders*. Australia: Surrey Beatty and Sons. pp 427–437.
- Rollinson J, Martin RD. 1981. Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. *Symp Zool Soc Lond* 48:377–427.
- Rose LM. 1994a. Sex differences in diet and foraging behaviour in white-faced capuchins (*Cebus capucinus*). *Int J Primatol* 15:95–114.
- Rose LM. 1994b. Benefits and costs of resident males to females in white-faced capuchins, *Cebus capucinus*. *Am J Primatol* 32:235–248.
- Rose MD. 1974. Postural adaptations in New and Old World monkeys. In: Jenkins FA, editor. *Primate locomotion*. New York: Academic Press. pp 201–222.
- Rosenberger AL. 1983. Tale of tails: parallelism and prehensibility. *Am J Phys Anthropol* 60:103–107.
- Rosenberger AL, Strier KB. 1989. Adaptive radiation of the ateline primates. *J Hum Evol* 18:717–750.
- Sanford R, Paaby P, Luvall J, Phillips E. 1994. Climate, geomorphology, and aquatic systems. In: McDade L, Bawa D, Hespenheide H, Hartshorn G, editors. *La Selva: Ecology and natural history of a neotropical rain forest*. Chicago: University of Chicago Press. pp 19–33.
- Schneider H, Rosenberger AL. 1996. Molecules, morphology, and platyrrhine systematics. In: Norconk M, Rosenberger AL, Garber PA, editors. *Adaptive radiations of neotropical primates*. New York: Plenum Press. pp 3–19.
- Schön Ybarra MA. 1984. Locomotion and postures of red howlers in a deciduous forest-savanna interface. *Am J Phys Anthropol* 63:65–76.
- Schön Ybarra MA, Schön MA. 1987. Positional behavior and limb bone adaptations in red howling monkeys (*Alouatta seniculus*). *Folia Primatol* 49:70–89.
- Strier KB. 1992. Ateline adaptations: behavioral strategies and ecological constraints. *Am J Phys Anthropol* 88:515–524.
- Sussman RW. 1991. Primate origins and the evolution of angiosperms. *Am J Primatol* 23:209–223.
- Turnquist JE, Schmitt D, Rose MD. 1997. Tail and body orientation during brachiation of captive *Lagothrix* and *Ateles*. *Am J Phys (suppl)* 24:230.
- Tyndale-Brisco CH. 1979. Ecology of small marsupials. In: Stoddart DM, editor. *Ecology of small mammals*. London: Chapman and Hall. pp 343–379.
- Youlatos D, Gasc J. 1994. Critical foraging locomotor patterns: head-first vertical descent in the red howler monkey (*Alouatta seniculus*). *Z Morphol Anthropol* 80:65–77.